

Feasibility of light-trapping in community research on moths: Attraction radius of light, completeness of samples, nightly flight times and seasonality of Southeast-Asian hawkmoths (Lepidoptera: Sphingidae)

JAN BECK* AND K. EDUARD LINSENMAIR

Dept. of Animal Ecology & Tropical Biology, Biocenter, University of Würzburg, Am Hubland, 97074 Würzburg (Germany)
jan.beck@gmx.net

Abstract: Experimental data and quantitative samples of Sphingid assemblages from tropical Southeast-Asia were analyzed to investigate methodologically relevant topics of light-trapping. Mark-Release-Recapture experiments revealed differences between lepidopteran families in the attraction radius of a light source, but no such differences could be found between 18 species within the family Sphingidae. Attraction radii (for 50% return rate within 5 minutes) were generally below 30 meters, which confirms results from previously published studies. Arrival of Sphingidae individuals at a light source was symmetrically distributed around midnight, and species differed significantly in median arrival time. No evolutionary hypothesis for such flight time differences (such as avoidance of interspecific mating or an effect of body size) could be confirmed from our data. At appropriately chosen sample sites (avoiding dense undergrowth), all-night sampling with a 125 Watt mercury-vapor lamp yielded more than $\frac{3}{4}$ of the expected species richness of Sphingidae in an average of 5-6 sample nights. Seasonality and temporal changes of local assemblages can probably be neglected for samples from largely non-seasonal regions like Borneo if data stem from a relatively short study time of a few years. In conclusion, (1) there are no indications that light trapping 'draws' specimens from distant habitats to the sampling site, (2) we did not find proof that species within the family Sphingidae are differentially drawn to light, which would lead to biases if light-trapping data are used as a measure of relative abundance in the habitat, (3) such biases, on the other hand, probably exist between taxonomically or morphologically more diverse taxa (e.g. for different families), and must be considered for a proper interpretation of results, and (4) light-trapping is an effective means of assessing species composition and relative abundances of Sphingid assemblages in Southeast-Asia, but sampling has to be carried out all night in order to maximize catch size and avoid biases due to different flight times of species.

INTRODUCTION

The use of artificial light sources is a commonly employed technique to attract night-active Lepidoptera for the study of taxonomy, biogeography and biodiversity (e.g. Holloway et al. 2001, Intachat & Woiwod 1999). While neither the physiological mechanism (Spencer et al. 1997, Sotthibandhu & Baker 1979, Hsiao 1973, Bowden 1984) nor the evolutionary significance (e.g. Holloway 1967) of this well-known attraction is known to a satisfying degree, it offers a number of advantages over alternative methods such as torchlight-transects (Birkinshaw & Thomas 1999), baiting with fruits, red wine (Süssenbach & Fiedler 1999, 2000), cheese or shrimp paste (S. Benedick & J. Hill, pers. com.), malaise traps (e.g. Butler et al. 1999), suction traps, rotary traps or other methods of passively sampling the air space (see Southwood

& Henderson 2000).

Light trapping yields a large number of specimens with a minimum of effort (Holloway et al. 2001, Fiedler & Schulze 2004). This is particularly true for automatic light-traps (see Southwood & Henderson 2000 for an overview of designs), which do not even require the presence of the researcher during trapping. However, some groups of Lepidoptera such as Sphingidae, which are the main subject of this study, have a tendency not to enter such traps in large numbers, but settle on the outside and in the perimeter of the light source. A comparison between data from automatic light-traps (Nasir Abd. Majid, pers. com.) and hand-sampling at light (own data) showed a ca. 30-fold higher yield for the latter method in lowland Borneo (see also Axmacher & Fiedler 2004, Brehm 2002). Thus, for the rest of this article, the term 'light trapping' refers to attracting moths with light, but sampling them by hand or net. Light can be assumed to sample the community more 'neutrally' than traps baited with food or pheromones, where specializations are more likely to occur. Last but not

* Corresponding author

Received: 21 October 2004

Accepted: 1 February 2005

least, light trapping allows sampling and killing most specimens relatively undamaged, an important requirement for precise species identification, which is not met by many 'passive' sampling techniques such as malaise or rotary traps.

On the other side, a number of objections to light trapping have been put forward, and Lepidopterists regularly face skeptic criticism by journal reviewers when publishing light-trapping research. The unresolved question of why moths actually come to light (see above for references) might further erode the scientific credibility of the method. The main arguments against light trapping in community ecology (see also Schulze & Fiedler 2003, Brehm 2002 for a more detailed discussion), as well as common responses to these arguments, are:

1) Light traps sample communities selectively rather than randomly. Besides measuring activity rather than relative abundance (see e.g. Wolda 1992, Simon & Linsenmair 2001), not all species are attracted to light to the same extent (Bowden 1982, Butler et al. 1999). Some species of hawkmoth are rarely or not at all attracted to light, but can be caught in numbers by other methods (e.g. Butler et al. 1999, Kitching & Cadiou 2000). Some species seem to be attracted only in parts of their range (e.g. *Daphnis nerii* comes to light in Africa, but not in Asia; I.J. Kitching, pers. com.). Females are generally rarer in light catches of Lepidoptera than males (see e.g. Brehm 2002 for data), which might reflect differences in activity as well as in attraction to light between the sexes. Janzen (1984) described arrival patterns of neotropical Sphingidae and Saturniidae at light and hypothesized on behavioral mechanisms leading to differences between taxa, sexes and age groups. Thus, it can be suspected that relative abundances of species at light are distorted by differential attraction to light and different levels of flight activity. While these potential problems are undeniable, their actual effect on the results of studies on the community ecology of moths remains to be quantified. Light trapping has often been proven to produce readily interpretable and ecologically meaningful results in studies on the biodiversity of Lepidoptera (e.g. Holloway 1976, Schulze & Fiedler 2003, Fiedler & Schulze 2004). Furthermore, the constraints of light trapping are shared with any other comparable sampling method (Schulze & Fiedler 2003, Southwood & Henderson 2000).

2) The effective attraction radius of light sources might be so large that moths are drawn from other habitats to a sampling site. Measurements of the attraction radii of light revealed distances of 3-250 meters (depending on study method and species; Muirhead-Thompson 1991, Bowden 1982), but attraction radii

are probably smaller than 30 meters in most situations for 'normal' light sources in entomological research (Butler & Kondo 1991, Muirhead-Thompson 1991). Furthermore, studies on the stratification of moth communities in the forest produced clear community differences between strata at height differences of 20-30 meters (e.g. Beck et al. 2002, Schulze & Fiedler 2003, Beck & Schulze 2003, using 15 Watt blacklight sources). Thus, while this is a common point of criticism, there is actually little indication that 'drawing' specimens to light from distant habitats really undermines the interpretability of samples.

3) The abundance of specimens at light is influenced by weather, lunar light and vegetation. While the effect of vegetation density around a sample site might be overestimated (Schulze & Fiedler 2003), effects of moonlight and weather (temperature, rain, fog, wind) have been clearly documented and discussed (e.g. Persson 1976, Muirhead-Thompson 1991, Holloway et al. 2001, Intachat et al. 2001, Yela & Holyoak 1997, McGeachie 1989, Brehm 2002). Generally, warm, moist and moonless nights produce highest specimen counts (as has been already noted by R. A. Wallace in 1869, pp. 95-97). Thus, raw abundances at light can never be used as reliable indicators of absolute population sizes in a region, but must be adequately 'converted' into figures which are comparable across samples with regard to the initial question of a study (Southwood & Henderson 2000).

Different light sources (power, wavelength) might also influence sample size and species composition (though this is mainly anecdotal; see Brehm 2002), as does the time of the night during which a trap is operated (e.g. Schulze 2000 found a steady decline in *Pyraloidea* specimens during the first 3 hours of the night in samples from tropical Borneo).

In an attempt to add new quantitative data to this discussion, two sets of questions were experimentally investigated in Sphingidae and other lepidopteran families in Southeast-Asia:

1) What distances of light attraction can we observe under 'real life' research conditions in a tropical habitat? This is particularly interesting for the Sphingidae - very large and extremely fast- and far-flying moths, which might thus be expected to exceed known figures of light attraction radii.

2) Is there evidence for differences in the attraction radius a) between Lepidoptera families with largely differing size, body shape and flight ability, and b) between species of the family Sphingidae? Such differences would be a clear indication that relative abundances of moths at light might present a distorted picture of real abundances, even if species which do not come to light at all (e.g. largely diurnal taxa such

Table 1: List of sampling sites in north-eastern Borneo where release experiments were conducted. Note that latitude and longitude are given in metric format. Additional sampling sites which were re-sampled and used for assessments of seasonality are both on canopy platforms in primary dipterocarp forests at Danum Valley (DV1 - N4.96°, E117.80°, Elev.: 220m a.s.l.), and at Poring Hot Springs in Kinabalu Park (POR1 - N6.04°, E116.70, Elev. 570m a.s.l.).

Site	Nights	Released	Latitude moths	Longitude	Elevation	Habitat a.s.l. [m]	Region
CRO1	9	285	5.44°	116.08°	1170	Ridge with road & planted banana fields, overlooking PF valley & mountains	Crocker Range Park
DV3	5	34	4.96°	117.86°	220	selectively logged (1988), opening along road	Danum Valley
DV4	6	134	4.97°	117.84°	340	selectively logged (1988/89), along road overlooking valley	Danum Valley
POR8	14	1.127	6.03°	116.77°	350	Local agricultural area near village	Poring Hot Springs

as *Macroglossum*) were not considered.

Furthermore, sampling data were analyzed to assess answers to the following general problems of sampling tropical insect populations:

3) What percentage of a local tropical community of hawkmoths can be sampled in a short-term light trapping program? While this question is not particular to light trapping but to any time-constrained ecological study, it is an important background figure to interpret light trapping results.

4) How does the nightly trapping time influence specimen numbers and species composition of samples? It has been suggested (e.g. Kitching & Cadiou 2000, Diehl 1982) that certain species can only be successfully caught at certain times of the night, but so far no quantitative data for whole local assemblages were available.

5) How does seasonality or other temporal change in the Sphingid assemblages of wet-tropical Borneo affect the credibility of results from short-time sampling of local assemblages? While it is often inferred from the climatological stability of tropical habitats that seasonal changes in communities are minute compared to temperate regions, significant effects of weather and season (mostly defined by rainfall) on insect populations have been shown (e.g. Schulze & Fiedler 2003, Süssenbach 2003, Intachat et al. 2001, Novotny & Basset 1998, Wolda 1978, 1988, Wolda & Flowers 1985, Tanaka & Tanaka 1982, Kato et al. 1995, Smythe 1985). Such effects are often ignored in ecological studies in the tropics, as time and logistic constraints do not usually allow for year-round, long-term sampling.

METHODS

a) Field methods

Attraction radius experiments

During two periods of field work in 2001/2002 and 2003, four suitable sampling sites in north-eastern Borneo (Sabah, Malaysia; see Table 1 for details) were chosen for release experiments. Site characteristics that influenced their choice were a high yield of Sphingid specimens (known from previous sampling), overall favorable logistic conditions and the existence of a straight stretch of logging road of at least 120 meters length. A generator-powered mercury-vapor bulb (125 Watt) was placed inside a white, cylindrical gauze-‘tower’ with a height of approximately 1.7 meters from the ground. Sampling was carried out in the period of reduced moonlight from a week before new moon until a week after new moon to maximize catch size. Nightly sampling was carried out from ca. ½ hour after sunset until ½ hour before sunrise, except if logistic problems made this routine impossible.

All arriving Sphingidae were hand-sampled from the light or nearby vegetation (<ca. 3 meter radius), measured (forewing-length), identified (Holloway 1987, D’Abrera 1986, Kitching & Cadiou 2000), and marked individually with a waterproof felt-tip pen on the dorsal forewing. Rare species were either killed and taken for closer taxonomical examination or stored inside the gauze cylinder for release at dawn, whereas common species (c. 14 specimens, see Table 2) were used for this study and released from random-

Table 2: List of all 24 species or *PU*s (1580 individuals) that were included in the release experiments. 18 species belong to the family Sphingidae, five species to the Geometridae and one to the Noctuidae. Some of the non-Sphingid *PU*s could not be reliably determined under field conditions and might refer to any of the species listed in the right column.

Family	Species	Individuals	Comments
Sphingidae	<i>Acherontia lachesis</i> Fabricius	42	
	<i>Acosmeryx anceus</i> Stoll	16	
	<i>Acosmeryx shervillii</i> Boisduval	70	
	<i>Ambulyx canescens</i> Walker	37	
	<i>Ambulyx moorei</i> Moore	38	
	<i>Ambulyx pryeri</i> Distant	49	
	<i>Ambulyx subtrigilis</i> Westwood	20	
	<i>Amplypterus panopus</i> Cramer	19	
	<i>Cechenena helops</i> Walker	40	
	<i>Daphnis hypothous</i> Cramer	211	
	<i>Marumba juvenis</i> Rothschild & Jordan	14	
	<i>Megacorma obliqua</i> Walker	20	
	<i>Psilogamma menephron</i> Cramer	147	
	<i>Theretra clotho</i> Drury	112	
	<i>Theretra latreillii</i> W.S. Macleay	49	
	<i>Theretra nessus</i> Drury	184	
	<i>Theretra rhesus</i> Boisduval	260	
	<i>Theretra silhetensis</i> Walker	18	
Geometridae (Ennom.)	<i>Biston</i> 3sp. Leach	31	<i>B. inouei</i> Holloway, <i>pustulata</i> Warren or <i>insularis</i> Warren
	<i>Celerena signata</i> Warren	22	
	<i>Dalima subflavata</i> Felder & Rogenhofer	36	
Geometridae (Geomn.)	<i>Pingasa chlora</i> Stoll	44	
	<i>Thalassodes</i> -complex (24sp.)	34	Genera <i>Thalassodes</i> , <i>Pelagodes</i> or <i>Orothalassodes</i>
Noctuidae (Aganainae)	<i>Asota</i> 4sp. Walker	67	<i>A. plana</i> Walker, <i>albiformis</i> Swinhoe, <i>heliconia</i> Linneaus or <i>egens</i> Walker
Σ Sphingidae		1346	
Σ Geometridae		167	
Σ Noctuidae		67	

lychosen distances along a logging road (distances in 5 meter steps, from 5 up to 120 meters, at one site up to 130 meters). After preliminary trials moth were transported to the release distance inside a plastic jar (500 ml) immediately after marking and released by turning the jar upside-down without giving the moths an initial flight direction. While this procedure carries the risk of non-directional, panicked flight rather than providing an ideal situation for deliberately choosing a flight direction, it avoided the effect that moths kept for a prolonged period after catching 'cooled down' after handling and often refused to fly at all when released, sitting in the same spot for hours. Catch time, release time and distance, and recapture time at the light were noted for all individuals. Each moth was released only once: after recapture it was stored

inside the gauze cylinder for release at dawn. Recaptures of marked specimens on following nights were not considered at all, but their occurrence at a rate of ca. 5 percent indicates that marking does not harm the moths (see also Beck & Schulze 2000, Beck et al. 1999). One species, *Daphnusa ocellaris*, was excluded from analysis as it was frequently observed trying to escape by crawling rather than by flight after handling (see discussion).

For a comparison between lepidopteran families, several *parataxonomic units* (*PU*s, Krell 2004) from non-Sphingid groups were chosen for their commonness and easy identification under field conditions (Holloway 1986, 1993, 1996). Three of these *PU*s contained several species in a genus, impossible to separate alive and in the field (see Table 2). These considerably

smaller and more delicate moths had to be caught, marked and handled with special care. Specimens which were accidentally injured were excluded from experiments.

Completeness of samples, flight time and 'seasonality' comparisons

Data for an assessment of the faunal completeness of short-time, high-intensity light trapping stem from an extensive sampling program in Southeast-Asia that was carried out from early 2001 to early 2004. Except for the four sites at which release experiments were conducted (see above) all sampling schedules were carried out independently of weather or moonlight conditions, so effects of these factors on abundance or flight time of moths should be randomly distributed. Generally, Sphingidae were hand-sampled (as described above) all night long for three to nine consecutive nights in a block. Median nightly sampling time was 10.2 hours. Sites with samples of less than 20 specimens within the first three nights were ignored. For the purpose of assessing the completeness of the applied sampling procedure we used data for 15 sites in north-eastern Borneo and one in Peninsular Malaysia. Sampling habitats ranged from primary forests through variously disturbed forest types to open, agricultural landscapes, from lowlands up to almost 1500 meters elevation. Sites were generally situated either in open areas or in the forest canopy (platforms or on cliffs or steep slopes) in order to maximize Sphingid catch (see Schulze & Fielder 1997). Four sites in Sabah (north-eastern Borneo) were re-sampled up to four times during the 3 year-study (see Tables 1 & 5, minimum 6 month between re-samples). These re-samples were used to assess effects of temporal change, but were considered as independent samples for the purposes of an evaluation of sample completeness, which raises the sample size to 23 sampling sessions.

At 11 sites in Borneo and one in Peninsular Malaysia, detailed arrival times of all specimens were measured (in 15 minute-steps: data from all sites were pooled for this analysis).

b) Methods of analysis

Return times of the experimentally released specimens ranged from a few seconds to more than eleven hours; about 47 percent of the released moths were not seen again at all during the night of release. Some specimens obviously did not directly return to the light, but flew around in the area and were later attracted to the light source again. Thus, we applied

the rule that only returns within five minutes from release were counted as '*returns*' for analysis, while any later arrivals were considered as '*non-returns*'. From speed measurements (100 meters in less than 20 seconds for several Sphingidae species) and direct observations of flight behavior we concluded that all species should be able to reach the light in that time interval even if they take some time to start or orient after release. Return rates per minute dropped rapidly within the first few minutes and reached a bottom level after about eight minutes (when 50% of all returning moths have come back to the light). Return rates after this point fluctuated apparently randomly (on a level of 0-2% return rate per minute) and probably represent released specimens which did not return directly to the light, but flew around in the area and entered the attractive radius of the light again at some later time, as described above. Preliminary analyses suggested that analysis with a five-minute return criterion yields a higher statistical power than longer return times (i.e., 8 min., 15 min.). After that time directional movements towards the light can probably not be expected any more.

Besides standard statistical procedures, the following methods of analysis were employed:

Loglinear Model

A loglinear model was used to test for influential factors on the frequency of *returns* vs. *non-returns*. Release distances were grouped into six 20 meter classes (5-20m, 25-40m, 45-60m, 65-80m, 85-100m, 105-120m), release distances >120m were not used for this analysis, as they were not available from all sites. A multi-dimensional contingency table, containing the frequencies of *returns* as well as those of suspected influential factors (such as release distance class, species identity), was constructed with all possible interactions between these factors, and then tested against the actual data (for a detailed description of loglinear models see StatSoft 2003).

Logistic Regression

As a second mode of analyzing the release experiment data we used logistic regressions (Trexler & Travis 1993). While carrying the disadvantage that not all data sets can be fitted well by logistic regression (predicting *return/non-return* better than random, see below), they allow assessing attraction radii (as the distance of 50 percent return-probability) in meters, rather than just comparing them on a class level.

The logistic equation (see e.g. Trexler & Travis 1993) was fitted to the *return/non-return* (1/0) data

(original data in 5 meter intervals). Regression values can be interpreted as probability for *return* (StatSoft 2003), the point of 50% return probability (x_i = *turning point* of the logistic regression for species i) is used as a measure of attraction radius. The variance of x_i is calculated from the variance of the regression parameters (b_0 , b_1) as

$$\hat{\text{var}}(\hat{x}_i) = (\hat{x}_i)^2 \cdot \left[\frac{\hat{\text{var}}(\hat{b}_0)}{(\hat{b}_0)^2} + \frac{\hat{\text{var}}(\hat{b}_1)}{(\hat{b}_1)^2} \right], i = 1, 2$$

For graphic display, 95% confidence intervals were assessed as $1.96 \cdot (\text{SD}(\hat{x}_i))$. For a more rigorous test of the hypothesis of a difference between two *turning points*, a z-test (StatSoft 2003) was used. Both the loglinear models and the logistic regressions were calculated with the computer program *Statistica 6.1* (StatSoft 2003).

Estimating total species richness

From the distribution of species in discrete samples an estimate of the total species richness at a site can be assessed by several methods (see Chazdon et al. 1998, Colwell & Coddington 1994, Colwell 2000, Melo et al. 2003). Of these, the non-parametric *Chao1*-estimator was used as it has proven robust in pilot studies (Chazdon et al. 1998, Peterson & Slade 1998) and yielded realistic figures in studies on temperate moths (Beck & Schulze 2003, Süssenbach & Fiedler 1999), where the total species richness is much better known than in tropical regions. Assessments of the species diversity of habitats by *Chao1*-estimates are often congruent to those with well established methods like Fisher's α or rarefaction curves (e.g. Beck et al. 2002, Schulze 2000). However, Brose & Martinez (2004) have concluded from simulation studies that in assemblages of species with variable mobility other estimators might perform better. In order to account for this finding, we additionally followed the suggested procedure of finding the 'optimal' estimator for the sample coverage at each site (calculated from the means of *ACE*, *ICE*, *MMMmeans*, *Chao1*, *Chao2*, *1st order Jackknife* and *2nd order Jackknife* estimators; see Brose & Martinez 2004). All species richness estimates were calculated with the computer program *EstimateS 5.01* (Colwell 2000).

The 'False Discovery Rate'-control of Benjamini & Hochberg (1995) was applied to avoid spurious significances due to multiple tests from the same data set, and all results which pass the criteria are marked

with an asterisk (*). However, it was not considered necessary to control analyses of different data sets, even if they overlap or are nested within another (see also Moran 2003).

Phylogenetic independence

Correlations of species' characters might not be statistically independent because of their common phylogenetic history (see e.g. Garland et al. 1999 for a review). The phylogenetic signal in data was tested with a randomization test (1000 runs), using the program *Phylogenetic Independence 2.0* (Reeve & Abouheif 2003, see also Abouheif 1999, Freckleton et al. 2002). Hawkmoth phylogeny was based on an updated version of the systematics in Kitching & Cadiou (2000, I.J. Kitching, pers. com.), allowing for unresolved nodes where applicable. To control for non-independent data, 'independent contrasts' (Felsenstein 1985) were calculated using the computer program *Phylop 3.61* (Felsenstein 2004; all branch length set to 1 except unresolved nodes, which were set to 0.0001).

RESULTS

1a) Release experiments: Loglinear models

A sample size of 1527 released moths was available for loglinear model analysis. The data structure was not suitable to include all interesting variables (return frequency, distance, species identity, family affiliation, experimental site) into one model. Therefore, certain variables were tested in separate models.

The first model analysis (see box 1) suggests that the research site had no influence on return frequencies, so data from different sites were pooled for all further analyses. Family affiliation of specimens had a clear influence on return frequencies (see 2nd model in box 1, figure 1), while for 18 species within the family Sphingidae no significant effect of species identity on return frequencies could be found (3rd model in box 1). All analyses show a significant effect of release distance on return frequencies. This was expected, since the frequency of returns should decrease with diminishing light intensity at larger release distances.

1b) Release experiments: Logistic regression

For the three families, as well as for twelve Sphingid species, logistic regression models could be constructed, while for six Sphingid species the models did not pass the χ^2 -test of a better-than-random prediction of the data. These species were consequently excluded

Box 1: Loglinear models**Model 1:** "Effects of research site" [site (4) x return (2) x release distance (6)] (*N*=1527)

Model 1	² (max. likel.)	df	p
Start model with 3 double-interactions	15.807	15	0.395
Best model (return-dist., site-dist. interactions)	18.715	18	0.410

Already the optimized model does not contain interactions of *research site* & *return frequency*.

Conclusion 1: No effect of site on return frequencies.

Model 2: "Effects of family" [*family* (3) x *return* (2) x *release distance* (6)] (*N*=1527)

Model 2	² (max. likel.)	df	p
Best model: 3fold- interaction fam. x return x dist	0	0	1
Exp. model 1: no 3-fold, but all 3 2-fold interactions	20.399	10	0.026*
Exp. model 2: no 3-fold and no fam.-return interaction	54.360	12	<0.0001*

The exclusion of the 3-fold interaction ("family influences distance-return interaction") leads to a significant difference between model predictions and real frequencies in data. Further exclusion of the family-return interaction brings another significant loss of predictive power of the model ($\chi^2_{df=2}=34$, $p<0.0001^*$).

Conclusion 2: Families have different return rates from different distances, i.e. different attraction radii. Beyond that, families differ in overall return rates (exp. model 1 *vs.* 2).

Model 3: "Effects of species" [species (18) x return (2) x release distance (6)] (*only Sphingidae*, *N*=1352)

Model 3	² (max. likel.)	df	p
Start model with 3 double-interactions	68.625	85	0.903
Best model (only return-dist interaction)	169.99	187	0.809
Exp. model without any interactions	298.73	192	<0.0001*

Conclusion 3: No effect of species identity (within the Sphingidae) on return frequencies is evident; already the optimized model does not include species. The exp. model only proves the essentially expected effect of release distance on return rates – otherwise the experiments would have been senseless.

from analysis. Figure 2 shows an example of a logistic regression for one species, figure 3 plots the attraction radii of the light (measured as the 'turning points' of the regression) and their estimated confidence intervals for the hawkmoth species.

On family level, 50% return rates vary between ca. 10-13 meters for Sphingidae and Noctuidae, whereas negative values for Geometridae were calculated due to very low overall return rates for *Pingasa* (5 returns of 44 releases) and particularly the small Geometrinae of the *Thallassodes*-group (5 of 34). Possibly handling effects have affected results in this very delicate group, although no obvious inability of flight was observed. The other Ennominae species showed attraction radii comparable to that of Sphingidae or Noctuidae (data not shown).

Turning points for Sphingid species vary between

26 meters and negative values (for species with very low return rates). Confidence intervals are large and indicate a high, unexplained variability in return behavior. For two species no variance of parameters could be calculated due to the structure of the data matrix. Maximum confidence estimates range up to 60 meters, which is still a value in reasonable boundaries of the literature for attraction radii of light (see e.g. Muirhead-Thompson 1991). No significant differences between species could be found for the 10 species for which testing was possible. Turning points of species do not correlate with the average body size of the species ($N=12$, $r^2=0.031$, $p=0.588$), whereas Fiedler et al. (unpublished) have found effects of body size on return rates in other, temperate Lepidoptera families.

Thus, the results obtained by logistic regression

confirm the analyses with the loglinear models.

2) Completeness of samples

During an average of 5-6 nights per sampling session, an average of more than $\frac{3}{4}$ of the *Chao1*-expected 'true' species richness could be collected (see Table 3 for details). Sampling success is weakly related to the number of sample nights as well as the number of sampled specimens, but not to observed species richness or diversity (as Fisher's α ; see figure 4 for test details).

Measurements of sampling success based on six other selected estimators of species richness (see methods) yield mostly quite similar figures, although Kendall's concordance coefficient for the seven estimators is surprisingly low at 0.173 and a Friedman-ANOVA indicates significant differences between estimator ranks ($N=23$, $\chi^2_{df=6}=23.85$, $p<0.001^*$).

An application of the method suggested by Brose & Martinez (2004) lead to the use of *ICE*, *1st* and *2nd* order *Jackknife* estimators, depending on the sample coverage for each site. However, overall results are very similar to *Chao1*-based estimates and indicate an average sample coverage of 77.3 percent.

Comparison with other samples from the region

In Table 4 the species richness (observed and expected) of the 23 standardized samples is compared to a combination of data from our own samples, published literature (Chey 1994, 2002, Holloway 1976, Tennent 1991, Zaidi & Chong 1995, Schulze 2000) and unpublished collections (Azmi Mahyudin and J.D. Holloway, pers. com.). These data vary in the use of different light types, sampling regimes and specimen numbers (local samples <20 specimens were not considered). Observed local species richness ranges up to 50 species (see figure 4: only samples with >1000 specimens contained over 40 species). Thus, the highest *Chao1*-estimate of 68 species (Table 4) is still in a realistic range. The slope of the data in figure 6 suggests that this may be close to the maximum local species richness that can be found by light-trapping in this region. Schulze et al. (2000) reported 59 night-active Sphingidae species from a compilation of data from several sampling sites within Kinabalu Park, Sabah. Higher records of local species richness in Southeast-Asia can probably only be found from continental regions (e.g. 67 species from year-round sampling on a site in northern Vietnam, T. Larsen, pers. com.), where regional species richness is higher than in insular Southeast-Asia (Beck & Kitching 2004).

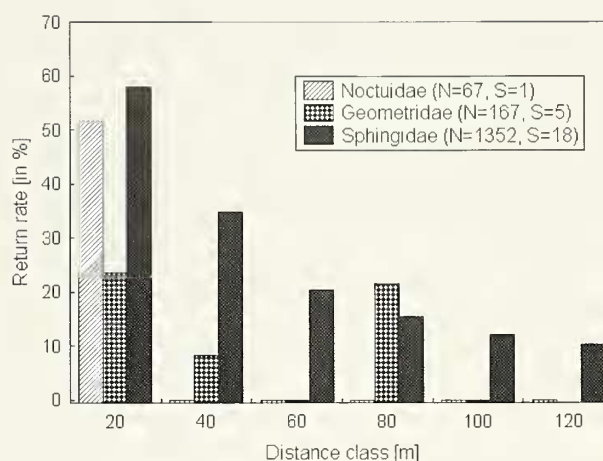


Figure 1: Return rates within 5 minutes (in percent) of three Lepidopteran families from six release distance classes (note that 'Noctuidae' contains only the genus *Asota*, see Table 2). Loglinear contingency table analysis (see box 1) indicates significant differences in return rates between the families.

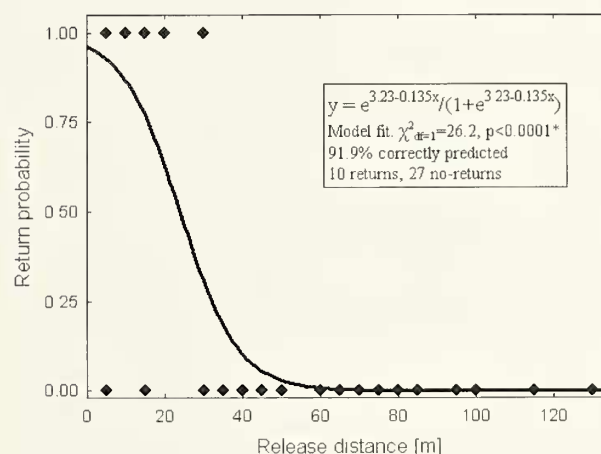


Figure 2: Exemplar logistic regression fit of the binary data (*return/non return*) for the Sphingid species *Ambulyx canescens* ($N=37$). Regression values (y-axis) range between 0 and 1 and can be interpreted as probability for 'return'. The 'attraction radius' (turning point of the regression curve = 50% return probability) is estimated at 23.9m for this species. Note that several data points may lie on the same position, which are not shown in the graph but influence the slope of the curve.

3) Flight time during the night

Figure 7 shows the distribution of arrival times of 1450 hawkmoths at 6 sample sites. Arrivals are clearly

Box 2: Z-tests for differences of logistic regression turning points (a) of families (b) of the most extreme species. Values in bold indicate significant differences ($z > 1.96$, $p < 0.05$).

a)

<i>z-value</i>	Sphingidae	Noctuidae
Noctuidae	-0.664	
Geometridae	2.173	2.418

b)

<i>z-value</i>	<i>A. shervillii</i>	<i>T. latreillii</i>	<i>T. rhesus</i>	<i>Asota 4sp.</i>
<i>T. latreillii</i>	1.469			
<i>T. rhesus</i>	1.024	-0.956		
<i>Asota 4sp.</i>	0.908	-1.112	-0.307	
<i>D. subflavata</i>	1.790	-0.295	1.094	1.436

Table 3. Mean values of 23 sampling sessions for the number of individuals (N), species (S), sampling nights, as well as the *Chao1*-estimate of true species richness (Colwell 2000), the proportion (in percent) of observed/estimated species richness (% S_{obs}), and the mean number of individuals per sampling night. The median is also given where distributions deviate from normality (KS-test, $p < 0.05$).

	Mean \pm SE	Median	Min.	Max.
N	220.9 \pm 48.5	116	25	847
S_{obs}	22.1 \pm 1.5		10	38
Nights	5.5 \pm 0.3		3	9
Chao1	30.1 \pm 2.5	28	14	68
% S_{obs}	75.9 \pm 3.2		37.9	94.4
N/night	35.9 \pm 6.5	26.2	6.2	121

Table 4. Species richness (observed and estimated) of local samples from Borneo and Peninsular Malaysia. See text for data sources of "all data".

	Samples	Mean	SD	Min	Max
S_{obs} (own)	23	22.1	7.4	10	38
Chao1-est (own)	23	30.1	12.1	14	68
All data S_{obs}	60	20.2	10.4	5	50

symmetrically distributed around midnight, with a steep rise in specimens in the third hour since sunset, and a decline after eleven hours. This is in marked contrast to smaller moths in Borneo or in temperate

regions (e.g. Thomas 1996, Schulze 2000, and own observations), which considerably decline in numbers after 2-3 hours past sunset.

Flight times clearly differ between species (figure 8). Median flight times also differ between Sphingid subfamilies, with Smerinthinae flying on average earlier in the night and Sphinginae later (KW-Anova: $H_{df=2} = 20.27$, $p < 0.0001^*$). However, median values for subfamilies are still quite tightly clustered around midnight (Smerinthinae 6h, Sphinginae 7.5h past sunset). Median arrival times also differ between sites (KW-Anova: $H_{df=11} = 130.8$, $p < 0.0001^*$), which is most probably the effect of different moonlight and weather conditions. Over the range of sample sites, however, these differences are leveled out as figure 7 shows a very symmetric distribution.

Assuming flight times are adaptive, two hypothetical factors can be tested with for an influence on flight time differentiation: a) Avoidance of mating in closely related taxa might be a reason for differences in activity patterns. Species within genera should have less flight time overlap than average species couples. b) With decreasing temperatures during the night, larger species can maintain their flight muscle temperature, hence their agility, more easily than small-bodied species.

Pianka's niche overlap of flight times was calculated for the 20 most commonly recorded Sphingidae species [$N_{per\ sp.} > 12$] as well as for intra-generic comparisons [$N_{per\ sp.} \leq 10$] within the genera *Ambulyx* [5 spp.], *Theretra* [4 spp.] and *Acosmeryx* [2 spp.] (see Southwood & Henderson 2000, computed with Programs for Ecological Methodology, Kenney & Krebs 2000). Mean values of niche overlap range around 0.57 for all Sphingidae and > 0.7 for the intra-generic comparisons. Thus, no indication for a lower overlap for within-genera comparisons was found. There is a tendency for smaller species to fly earlier than large species ($N = 49$, Pearson's $r^2 = 0.109$, $p = 0.021$; body size was measured as mean forewing length, which is a good surrogate for body mass within a group of similar body architecture; Loder et al. 1998, Schoener 1980). However, a clear phylogenetic signal was detected in body size data (randomization test: $p = 0.001^*$ for phylogenetic independence), whereas no signal was detected in flight time data ($p = 0.430$). A correlation of independent contrasts for body size and flight time is not significant ($N = 48$, $r^2 = 0.017$, $p = 0.376$), nor is a correlation of contrasts for body size with 'raw data' for flight time ($N = 48$, $r^2 = 0.002$, $p = 0.769$), using contrasts for a neutral, star-like phylogeny (see also Rheindt et al. 2004 for methods). These analyses indicate that the weak relation between flight time and body size (see above) must be considered spurious under the

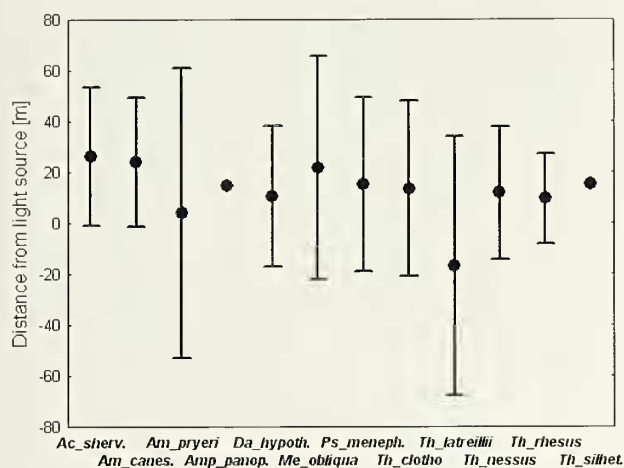


Figure 3. 'Turning points' of logistic regressions for Sphingidae species, which indicate the distance of 50 percent return-probability ($\pm 1.96SD$) after experimental release. No significant differences can be found between the species.

above described assumptions.

4) 'Seasonality' and temporal change

Comparisons of the 'within-habitat' diversity of re-sampling sessions (figure 9) showed a remarkable constancy of measures; only at one site (CRO1) a significant change in diversity could be observed, even though the species inventory in both samples was identical (Table 6). No influence of 'seasons' (see Table 5) on diversity differences could be observed, indicating that changes in the structure of hawkmoth assemblages are either random or directional in a longer time scale than one year (Beck et al., 2006). Measures of between-session similarity of sampled assemblages are relatively high, particularly for NESS-indices (Grassle & Smith 1976) which are not biased (towards lower values) by incomplete speciesinventories as Sørensen-indices are (Southwood & Henderson 2000). If common species are weighted high for calculation of $NESS(m=1)$, it seems that primary forest sites (DV1, POR1) are more stable than disturbed sites. This pattern, however, breaks down if rare species are weighted higher at $m=21$. All $NESS(m=21)$ -values are >0.82 for within-site comparisons of sessions (as e.g. in Novotny et al. 2002). Multidimensional Scaling (figure 10) of $NESS(m=21)$ -values illustrates that faunal differences between seasons are mostly smaller than those between sites. The sampled assemblages were tested for spatial and temporal differences (see Table 5 for classification) by the randomization test

Analysis of Similarity (ANOSIM), using PRIMER 5 (2002). In one-way designs, significant effects could be found between sites (Global $R=0.711$, $p=0.001^*$), but not between seasons (Global $R=0.043$, $p=0.552$) or sampling year (Global $R=0.026$, $p=0.397$). Furthermore, in various two-way designs (including nested designs) no temporal effects (season or year) could be found.

Relative abundances of sampled species were correlated to each other (Table 7) to assess how well sampling in one session reflects the rank order of species in other sessions at a site. All relevant correlations are highly significant, though R^2 -values are not particularly high. Within-site correlations have significantly higher R^2 -values than between-site correlations (t-test: $t_{df=53}=7.47$, $p<0.0001^*$).

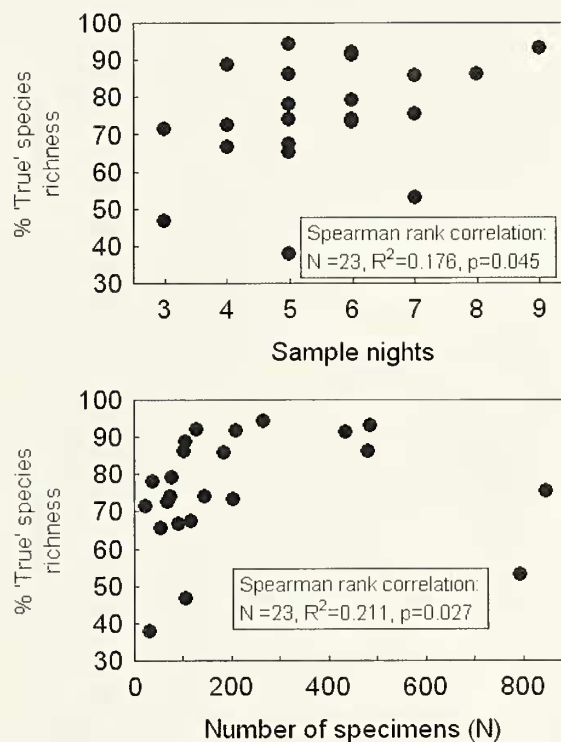


Figure 4. Correlations between the number of sample nights (upper graph) and the number of sampled individuals (lower graph) and the percentage of sampled 'true' species richness (based on *Chao1*-estimates, Colwell 2000). Each dot refers to a different sampling session, not to sub-samples from the same sampling session. No correlations were found with the observed number of species (S_{obs} : $N=23$, $R^2=0.012$, $p=0.614$) and the species diversity (Fisher's $\hat{\alpha}$: $N=23$, $R^2=0.084$, $p=0.179$).

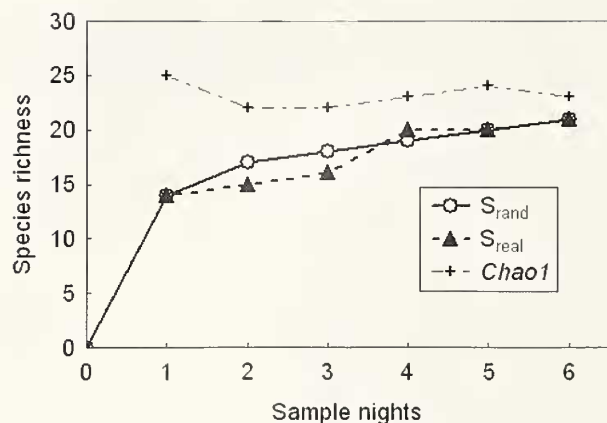


Figure 5: Exemplar species accumulation curves for a 'good' sampling site at Danum Valley, Borneo (DV1-I): After 6 nights of sampling, 21 of 23 estimated species were caught (91.3% sampling success). S_{rand} is smoothed by a 100-fold randomization of the sample night order (Colwell 2000), $Chao1$ is the estimate of total species richness at the respective number of (randomized) sampling nights. The $MMMeans$ estimator (Colwell 2000), which fits an asymptotic curve to the randomized species accumulation curve, yields an estimate of 22 species for this site. The total number of specimens at this sampling session was 437.

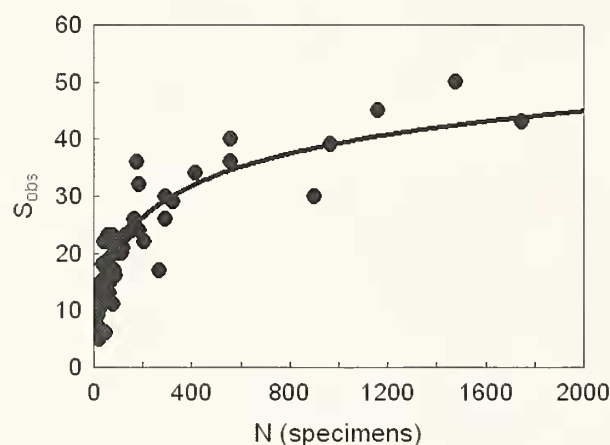


Figure 6: Observed species richness of Sphingidae as a \log_{10} -function of the number of sampled specimens for 60 local light-trapping samples from Borneo and Peninsular Malaysia (see text for data sources). The data are significantly correlated ($N=60$, Pearson's $r^2=0.839$, $p<0.0001^*$).

DISCUSSION

Attraction radius of light sources

In the experimental part of this study we showed

for 18 species of Sphingidae, as well as some species of the Geometridae and Noctuidae, that the effective attraction radius of a 125 Watt MV-lamp is indeed relatively low with mean attraction distances below 30 meters. This confirms what most previous studies found with different methods, species and habitats (e.g. Muirhead-Thompson 1991, Bowden & Morris 1975, Onsager & Day 1973, Plaut 1971, Meineke 1984, Kovács 1958). Even for hawkmoths, which probably form the upper limit of lepidopteran flight strength and speed, there is no indication that light trapping draws moths from distances so great that investigations on local habitats were 'polluted' by specimens from far away. Occasionally specimens were found at light sources far from their typical habitat (e.g. on ships far off the nearest coast; I.J. Kitching, pers.com.), but there is no indication whatsoever that such specimens were artificially drawn out of their natural habitat by the light. Due to dispersal and migratory behavior some few individuals of a species will always show up away from its breeding habitats, but such 'strays' are not *per se* an artifact of sampling.

Differences between taxa

A comparison between families with considerably different body sizes and shapes revealed significant differences in return behavior and attraction radius. Fiedler et al. (unpublished data, pers. com.) found in similar mark-release experiments in Germany that body size has a significant effect on return rates of Geometroidea (though not in other taxa). Therefore, results of light trapping studies from taxonomically and/or morphologically very diverse samples must be viewed very carefully, as relative abundances at the light might not reflect relative abundances under natural flight conditions across all taxa. Within the relatively uniform taxon Sphingidae, on the other hand, comparisons of 18 species did not show any non-random differences in return behavior despite a considerable sample size (over 1300 released specimens, see Table 2). While it is known that some differences between species must exist (e.g. some species do not come to light at all; Butler et al. 1999 found substantial differences between blacklight and malaise traps for three North American hawkmoth species), these differences might often be diluted beyond significance by a high variability in attraction radii (see below) during natural trapping conditions. It might be argued that in this study the concentration on relatively common species (for the obvious reason of attaining sufficient sample sizes) might have neglected systematic differences between common and rare species. Generally, a lack of an effect is never proof of

its non-existence, but there is presently no indication to assume a systematic difference in attraction radius between rare and common species.

The species-abundance distributions in a large number of light-trapping samples of hawkmoths from Southeast-Asia fit the lognormal distribution very well (Beck, 2005). This or similar mathematical distributions have been found in samples of a large number of organisms (e.g. Tokeshi 1993), including light-trap samples of moths (e.g. Robinson 1998) as well as data from sampling procedures that are beyond any doubt free of sampling errors (e.g. counting tree seedlings in sample squares, Hubbell 2001). If the lognormal and related distributions have any biological significance (e.g. Hubbell 2001, Hengeveld & Stam 1978) and are not merely a statistical characteristic inherent to any heterogeneous data set, then massive biases of light trapping would have distorted this relationship for night-active Lepidoptera sampled in this way.

High variability in data: A methodological artifact?

The release experiments revealed a large variation in return behavior that was also evident from observations during field work. While some specimens were seen flying in a straight line towards the light after release at distances of up to 130 meters, other specimens did not return at all. The failure to find species-specific differences in light attraction might be attributed to this variability rather than homogenous measures of attraction (see e.g. figure 3). Therefore it is a crucial question for the interpretation of results to what degree such variation might be caused by handling effects or other problems of the experimental design. Obvious handling effects could repeatedly be observed in *Daphnusa ocellaris*, which walked away after release rather than trying to fly, and was consequently excluded from all analyses. However, it was not completely surprising to find odd behavior in this species, as it is an 'unusual' hawkmoth in a number of other behavioral traits: In Borneo, it is the only species that is frequently encountered in the undergrowth of the forest, while all other species tend to fly in the open airspace above the tree canopy (Schulze & Fiedler 1997). Furthermore, its relatively small thorax makes it considerably weaker in beating its wing than species of comparable size (pers. obs. during handling). The observed behavior can probably be interpreted as a predator escape tactic after an unsuccessful first attack of a bat. In no other Southeast-Asian hawkmoth species was such behavior observed.

Predation by bats around the light was high, and occasionally released moths were caught by bats just before returning to the light (pers. obs.). While

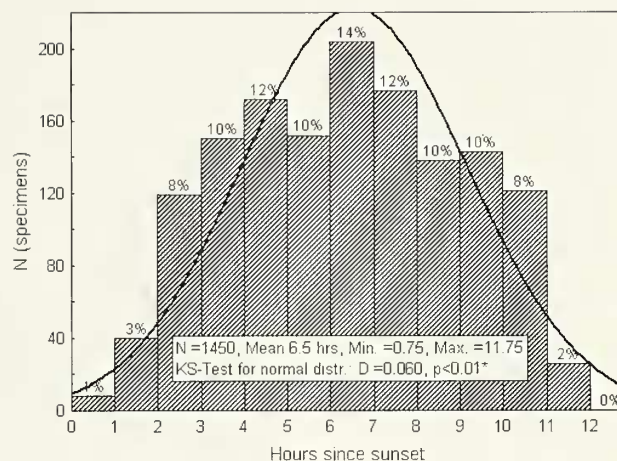


Figure 7: Frequency distribution of arrival times of Sphingidae specimens in Borneo and in Peninsular Malaysia as a function of sampling time. Despite a symmetric distribution around midnight data do not fit a normal distribution.

this reflects the situation at most trapping sites in Southeast-Asia, it might mean that 'physiological' attraction radii are slightly larger than 'ecological', bat-influenced measures of the radii. Weather, moonlight and temperature varied within as well as between sampling nights and might be responsible for a large part of variation in measured attraction radii. All three parameters are known to influence total catch size (e.g. Yela & Holyoak 1997) and might be suspected to influence the flight activity of moths as well as the attraction radii of light sources. Fiedler et al. (pers. com.) found effects of temperature on attraction radii of Geometroidea in temperate Germany, where temperatures vary much more than in tropical lowland areas. However, just like bat predation, such variability only reflects realistic sampling conditions and is therefore not a methodological problem. Whatever physiological differences there might be to influence differences in response to light between species, natural variation in conditions during realistic sampling procedures seems to reduce them to a non-directional 'noise' that will most probably not produce any artifact results in ecological studies.

Completeness of samples

Using the *Chao1*-estimator (Colwell 2000) as a measure of true species richness, we found that short term (<10 nights), high intensity light trapping (125W MV-lamp, all night hand-sampling) can yield a surpris-

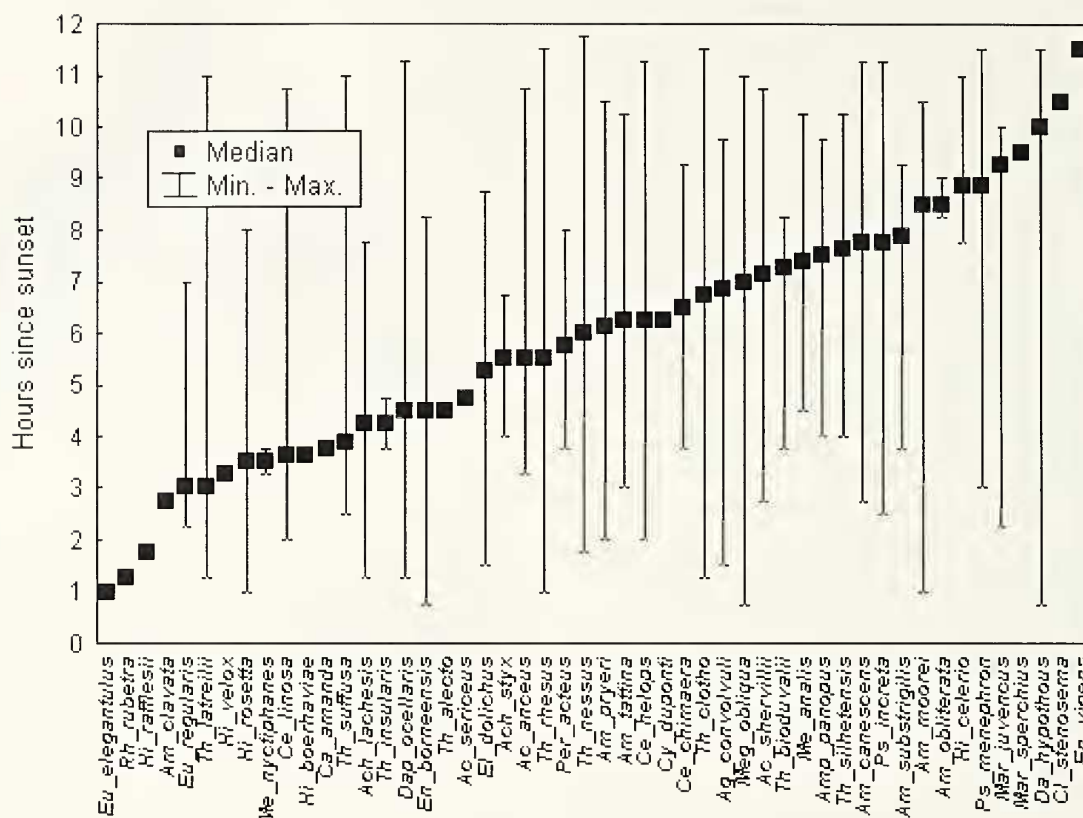


Figure 8: Median, earliest and latest arrival times of 50 Sphingid species in Borneo and Peninsular Malaysia (N=1450). A KW-Anova of the 24 species with individual numbers e"10 indicates that different species have clearly and significantly differing flight times during the night (N=1375, $H_{df=23}=509.04$, $p<0.00001^*$).

ingly complete picture of the species assemblage that is present in a habitat at a particular time (excluding the day-active taxa, of course). An average of $\frac{1}{3}$ of the expected species (and often much more) could be inventoried with this method. Sphingidae are not a very speciose taxon in Southeast-Asia (e.g. species numbers from Borneo: 113 Sphingidae (Beck & Kitching 2004), compared to ca. 1000 described Geometridae (Holloway 1993, 1996, 1997)), but a relatively high degree of available 'background information' even for tropical species (taxonomy, distribution, host plants: Kitching & Cadiou 2000) renders them a very attractive group for ecological research within the Lepidoptera.

It is difficult to judge how reliable species richness estimates really are. *Chao1*-estimates increased with increasing S_{obs} within some sites (see Schulze & Fiedler 2003 for a similar effect on Fisher's α of Pyralidae), even though they often reached relatively stable values with addition of the last 1-2 sample nights (see e.g. figure 5). Alternative estimators (see results) came to very similar figures of expected species, and figure 6 indicates that extrapolation estimates are generally in

a realistic range. Particularly, 'optimal estimators' according to Brose & Martinez (2004) correlate well with *Chao1* (Spearman rank correlation: $N=23$, $R^2=0.525$, $p<0.00001^*$) and lead to an overall very similar assessment of sampling success. Thus, estimates are considered credible, although only more empirical studies on Colwell's (2000) estimators can really judge their value as predictors of true species richness.

Moreno & Halffter (2000) used randomized species accumulation curves to determine asymptotes of species inventories for Neotropical bat assemblages, which were suggested to be used for the comparison of incomplete samples, across different sampling methods or sampling efforts. This was criticized by Willott (2001; but see Moreno & Halffter 2001), who pointed out that (1) the number of sampled individuals is a better measurement of sampling effort than the number of sampling units, and (2) the method is not suitable for high diversity taxa where only a small fraction of a local assemblage has been sampled. The *MMMeans* method of richness estimation (Colwell 2000, Chazdon et al. 1998) follows a

similar approach by fitting an asymptotic Michaelis-Menten type curve to randomized species accumulation curves. *MMMeans*-estimates were generally very similar to *Chao1*-estimates in this study. Figure 5 shows an example of species accumulation curves. Estimates of total species richness from *Chao1* were in an acceptable range when viewing randomized species accumulation curves, which adds credibility to both approaches.

Flight times

The analysis of flight times shows that it is crucial to stay out all night in order to sample Southeast-Asian hawkmoth communities successfully and completely. Not only does the greatest number of specimens come around midnight to the light (and moths keep coming until dawn), but a shorter sampling period would also systematically under-represent certain species, as median flight times vary significantly between species. The ability of Sphingidae to warm up their flight muscles by shivering gives them the ability to make their flight activity relatively independent of ambient temperatures, at least under the moderate temperature changes of a tropical night. However, in other tropical moth taxa empirical data prove that numbers of moths arriving at night decrease after the first few hours (Schulze 2000, Brehm 2002, Süssenbach 2003). Hence, the judgment stated above might not be valid for such taxa, and the 'coverage' of the assemblage in samples may be considerably higher even if sampling is carried out only for parts of the night.

It remains to be seen from similar data on other taxa, if 'niches' in flight time are a general feature of moth assemblages. Anecdotal information points into this direction – Southeast-Asian Saturniidae, for example, are found in numbers only after midnight (pers. obs., see also Janzen 1984). No ecological reasons for temporal niche segregation could be confirmed from our data, though early-flying taxa tended to be smaller than late-flying ones. Studies on other organisms suggest that partitioning of activity times is only rarely caused by competition or predation, and that endogenous rhythmicity may be an evolutionary constraint (e.g. Kronfeld-Schor & Dayan 2003). We did not find any decline in the number of Sphingidae specimens (nor for other groups, though this was not quantified) under conditions of heavy rain. No moths might be flying during the peak minutes of a tropical rainstorm, but they still keep coming under very unpleasant sampling conditions. Thus, breaks from a sampling schedule due to heavy rain (which are commonly reported in the literature) cannot be excused by low sampling success, although more

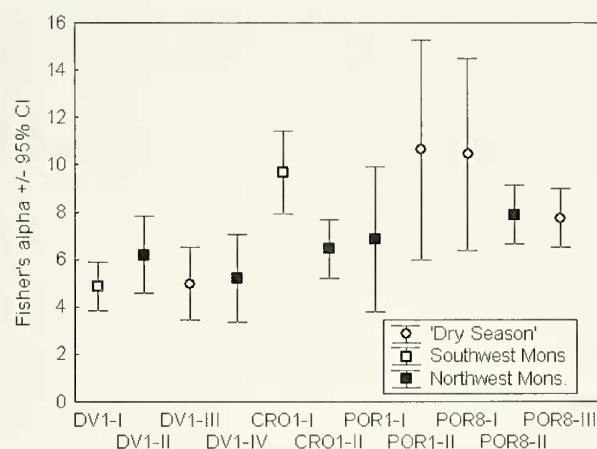


Figure 9: Fisher's α ($\pm 95\%$ confidence interval) as a measure of within-habitat diversity for re-samples of four sites in north-eastern Borneo (see Table 1). Only at one site (CRO1) a significant difference in diversity between re-samples within a site (dashed lines) can be observed. There is no indication for systematic influences of season (see Table 5) on diversity. Fisher's α ($\pm 95\%CI$) for pooled sample sessions are: DV1: 5.98 ± 0.99 , CRO1: 8.15 ± 1.23 , POR1: 8.65 ± 2.46 , POR8: 7.97 ± 1.05 . All samples fit the *logseries*-distribution sufficiently good to justify the use of Fisher's α (Southwood & Henderson 2000).

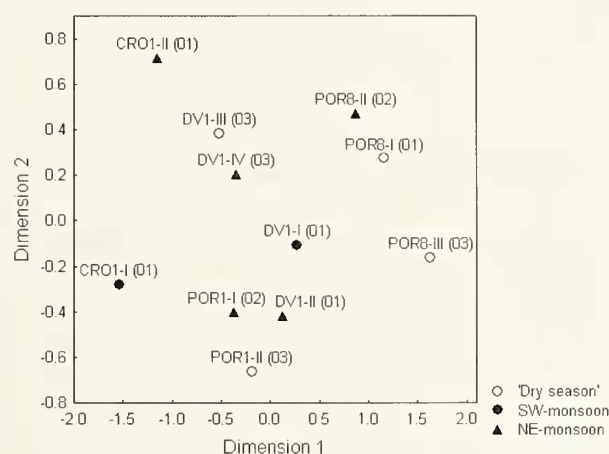


Figure 10: Multidimensional Scaling of NESS($m=21$)-values ordinate sampling sessions according to their faunal similarity. Different symbols indicate season (see Table 5 for classification), labels give sample acronyms and the year of sampling (in brackets). Temporal differences (season, year) do not produce meaningful patterns, whereas samples are differentiated according to site affiliation (see text for randomization test).

fragile taxa might be damaged beyond identification by wet equipment.

Table 5. Timing of re-sampling sessions (4-9 nights each) at four sites in Sabah, Borneo. Numbers in brackets indicate 'seasons' based on rainfall measurements at Danum Valley Field Centre (see Marsh & Greer 1992), but our assessment of seasons is based on means of 17 instead of 6 years of meteorological data collection (data not shown, G. Reynolds pers. com.): (1) = 'Dry Seasons' February-April, July-September (<230 mm rainfall per month), (2) = 'South-West Monsoon' May-June, (3) = 'North-East Monsoon' October-January (>250 mm). Climate patterns might differ between parts of Borneo island, see also Walsh & Newbery (1999), Kato et al. (1995), Kitayama et al. (1999).

Site	Sample I	Sample II	Sample III	Sample IV
DV1	Jun 2001 (2)	Dec 2001 (3)	Mar 2003 (1)	Dec 2003 (3)
CRO1	May 2001 (2)	Nov 2001 (3)		
POR1	Jan 2002 (3)	Feb 2003 (1)		
POR8	Jul 2001 (1)	Jan 2002 (3)	Feb 2003 (1)	

Table 6. Measures of between-sample diversity between sampling sessions at four sites in Borneo. All indices range from 0 (no species in common between sessions) to 1 (identical samples). While Sørensen-indices consider only presence-absence data (Southwood & Henderson 2000), NESS-indices (Grassle & Smith 1976) use quantitative data with increasing weight on rare species with increasing m (see e.g. Brehm & Fiedler 2004 for an assessment of between-habitat diversity measures). For comparison between-sample diversity of 10 samples (within 12 months) in seasonal northern Vietnam (Hoang Lien Nature Reserve, data from T. Larsen, pers.com.) is presented.

Site	Re-samples	Sørensen (Mean±SD)	NESS ($m=1$) (Mean±SD)	NESS ($m=21$) (Mean±SD)
DV1	4	0.83 ± 0.18	0.95 ± 0.04	0.85 ± 0.09
CRO1	2	1.00	0.80	0.95
POR1	2	0.67	0.86	0.94
POR8	3	0.87 ± 0.12	0.78 ± 0.07	0.92 ± 0.07
HOA	10	0.47 ± 0.24		

Seasonality and temporal change

We have found no evidence of 'seasonality' in Sphingid assemblages from north-eastern Borneo, though our data were too limited for an application of rigorous tests of cyclic patterns (e.g. Wolda 1988). Previous studies suggested that not only in tropical habitats with clear wet and dry seasons (e.g. Frith & Frith 1985, Janzen 1993), but also in less seasonal regions (Novotny & Basset 1998, Intachat et al. 2001, Wolda 1978) insect abundances can fluctuate considerably as an effect of changes in precipitation. Our data suggests that while there are considerable changes of relative and absolute abundances of individual species between sampling sessions (see below), measures of diversity (figure 9), community structure (Table 6) and the rank order of species (Table 7) are not dramatically different. A number of other studies also concluded that temporal changes did not affect measures of community structure for studies of ants in Borneo (Brühl 2001) or Lepidoptera in Sulawesi (Barlow & Woiwod 1993), New Guinea (Novotny et

al. 2002) and Borneo (e.g. Fiedler & Schulze 2004, Schulze & Fiedler 2003). Thus, in the absence of clear seasonal patterns (see also Walsh & Newbery 1999), we conclude that short-term samples probably give reasonably good data for analyses of local assemblages of Sphingidae in Borneo – even though it has to be kept in mind that assemblages might change over timescales of several years (Beck et al., 2006). For a few species (*Theretra rhesus*, *T. latreillii*, *T. insularis*, *Daphnis hypothous*, *Marumba juvencus*, *Enpinanga borneensis*, *Cechenena lineosa*) we have indications of larger long-term population fluctuations from the re-samples in our data as well as in comparison with older literature (e.g. Holloway 1976, 1987, Tennent 1991).

CONCLUSIONS

From the experimental and empirical data that we presented above, the following conclusions and methodological advice can be drawn:

1) For complete and efficient sampling of Sphingidae (at least in Southeast-Asia), hand-sampling

Table 7: R-values for Spearman rank correlations of relative abundances of species across 11 (re-)sampling sessions in Borneo. All correlations have p-values <0.05* (N=58), values in bold print mark correlations at p<0.0001*. The latter include all within-site correlations of sessions (in boxes).

	DVI-I	DVI-II	DVI-III	DVI-IV	CROI-I	CROI-II	PORI-I	PORI-II	POR8-I	POR8-II
DVI-II	0.812									
DVI-III	0.673	0.624								
DVI-IV	0.650	0.701	0.576							
CROI-I	0.555	0.572	0.465	0.515						
CROI-II	0.493	0.586	0.379	0.410	0.740					
PORI-I	0.603	0.650	0.577	0.525	0.657	0.621				
PORI-II	0.598	0.643	0.504	0.425	0.525	0.549	0.676			
POR8-I	0.359	0.430	0.272	0.274	0.419	0.388	0.309	0.393		
POR8-II	0.425	0.510	0.395	0.409	0.422	0.458	0.538	0.474	0.767	
POR8-III	0.373	0.441	0.370	0.400	0.478	0.449	0.453	0.534	0.775	0.842

at a light source during the whole night is necessary. Shorter nightly sampling sessions miss a considerable number of specimens, and – more importantly – might specifically miss species with particular flight times, which would bias data. However, as long as sampling is kept standardized across habitats to be compared, and provided that the samples are sufficiently large and representative (e.g. by sampling during the peak hours of activity around midnight) between-site comparisons might still yield valid results.

2) Under these conditions, a week of sampling will usually yield over 100 specimens, which often represent more than ¾ of the expected species in a habitat (excluding day-active species). Pre-condition to this is an adequate choice of sampling site, which should sample from some open airspace rather than dense vegetation (Schulze & Fiedler 1997). Seasonality of assemblages can probably be neglected for practical purposes, though care has to be taken when including data from older sources or from more seasonal regions.

3) There is no indication that a significant fraction of specimens are not sampled locally, but drawn from some distant natural habitats to the sampling site by the light. A 125 Watt mercury-vapor bulb has a 50% attraction radius of less than 30 meters (which confirms older measures from the literature), so even highly active, fast-flying taxa such as Sphingidae can be very locally sampled. However, individual specimens might fly far from their normal (breeding) habitat for natural reasons (e.g., dispersal, migration).

4) No evidence was found that species within the family Sphingidae differ significantly in their attraction to light. While this does not generally rule out that such effects may occur, natural variation of sampling conditions will effectively level out such subtle

differences. We tentatively conclude that abundances at light sources do largely reflect relative abundances (or rather flight activity) in a habitat. However, wherever there is an option of comparing relative abundances at light with other measures of relative species abundance (e.g., counts of caterpillars from random samples) these should be employed and critically discussed.

5) There is indication that attraction towards light sources differs between higher taxonomic units such as Lepidopteran families. Large differences in body size or shape might be a key predictor for the dimension of such differences. Data for taxonomically or morphologically diverse assemblages should be critically explored for potential biases resulting from different attraction radii of light. In biodiversity studies that compare different habitats, for example, it should be explored whether different taxonomic sub-units follow similar patterns before they are presented as one common trend from a pooled data set.

ACKNOWLEDGEMENTS

We thank Dr. Chey Yim Khen (Forest Research Centre of Sabah, FRC), Dr. Jamili Nais and Maklarim bin Lakim (Sabah Parks), Peter Chong (DVMC, Innoprise Inc.), Glen Reynolds and Dr. Rory Walsh (Royal Society), Intraca Woods Inc. and Henry Barlow (Genting Tea Estate) for productive cooperation and/or for granting permission to sample on sites under their respective control. Furthermore, we thank the Economic Planning Unit (EPU) of Malaysia for granting a Research Permit for Malaysia, and the British Royal Society for accepting this project as part of their Southeast-Asian Rainforest Research Project (SEARRP). Dayang Siti Nortasha (Universiti Malaysia Sabah) and Katrin Blassmann (Universität Würzburg) helped with the mark-release experiments. Dr. Ian J. Kitching (NHM, London) helped with the identification of specimens and methodological advice. Furthermore, we thank Dr. Konrad Fiedler, Dr. Christian H. Schulze and Dr. Jeremy D. Holloway for helpful comments and discussions. Two anonymous reviewers gave

very helpful comments on an earlier draft of the manuscript. The study was financially supported by the 'Graduiertenkolleg' of the German Research Council (DFG, 'Grundlagen des Arthropoden-verhaltens'), the 'Sys-Resource' program of the European Union and by a Ph.D.-scholarship of the German Academic Exchange Service (DAAD).

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